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Biometric analysis of lacustrine and riverine populations of *Palemonetes antennarius* (H. Milne-Edwards, 1837) (Crustacea, Decapoda, Palaemonidae) from north-western Greece

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Abstract

Comparative study of morphometric measurements was undertaken on populations of *Palaemonetes antennarius* from two freshwater habitat zones (lacustrine pelagic and lacustrine littoral) and from the fluvial littoral habitat zone of three estuaries of north-western Greece. Multivariate statistical analyses (principal component analysis and discriminant function analysis) revealed clear morphometric differences between sexes and sampling sites. The observed differences are expressed mainly thought the measurements related to the body heights (carapace height and second pleon height), as a result of sexual dimorphism, High values for the female body heights seem to be correlated to specific fecundity profile and reproductive strategy. On the other hand, morphometrical variables related mainly to body lengths, such as rostral, telson and pleon lengths, were observed to be correlated to the study sites. Characters related to the summing capacity (telson length, telson width and pleon lengths) were generally found to have higher values in the specimens from habitats with high reophilic profile.
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Keywords: Biometry; *Palaemonetes antennarius*; Decapoda; Palaemonidae; Freshwater habitats; Estuaries; Stock discrimination

Introduction

Multivariate morphometrics have successfully been employed in population studies, stock discrimination, biogeographical studies and phenotypic plasticity (Von Cramon-Taubadel et al. 2005). In particular, functional morphometry has been used in a number of studies for natant decapods in order to compare geographically isolated populations (De Grave and Diaz 2001; Tzeng 2004; Tzeng et al. 2001), to elucidate intraspecific variation (De Grave 1999; Kapiris and Thessalou-Legaki 2001) and to study the morphological determination of body by rearing habitat (Maynou and Sardá 1997; Anastasiadou and Leonardos 2008).

Particularly, the Caridean family of Palaemonidae is a group that demonstrates a peripheral distributional pattern (Bânârescu 1990), colonizing freshwater and estuarine habitats, surface or subterranean waters (Bânârescu 1990; Udekem d'Acoz 1999). In the Atlanto-Mediterranean zoogeographical area, the genus *Palaemonetes* Heller, 1869 is represented by six species: the estuarine Atlanto-European *Palaemonetes varians* (Leach, 1814) (Lagardére 1971; Noël 1992; Udekem

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d'Acoz 1999), the freshwater endemic of eastern Spain *Palaemonetes zariquieyi* (Sollaud 1939; Zariquiey Alvarez 1968), the freshwater Tunisian *Palaemonetes mesogenitor* (Sollaud, 1912) (Sollaud 1939; Azzouna 1994), the freshwater Syrian *Palaemonetes mesopotamicus* Pesta, 1913 (Pesta 1913; Sollaud 1939), the freshwater Turkish *Palaemonetes turcorum* Holthuis, 1961 (Holthuis 1961) and finally the Mediterranean endemic *Palaemonetes antennarius* (H. Milne-Edwards, 1837) (Holthuis 1961; Froglia 1978; Koçataş 1981; Cottiglia 1983; Noël 1992; Gottstein Matočec and Kerovec 2002; Gottstein Matočec et al. 2006). In Greece, *P. antennarius* has been reported from Ionian Islands (Korfu and Zakynthos; Holthuis 1961), Aegean Islands (Crete, Kos and Rhodes; Santucci 1928; Holthuis 1961; Lewinsohn 1976; Anastasiadou et al. 2002), and western Greece (Udekem d'Acoz 1999; Anastasiadou et al. 2002, 2005).

Despite the already known geographical distribution of *P. antennarius*, significant information on the bionomic traits of the species has been also documented. *P. antennarius* is a euryhaline (Parry and Potts 1965; Dalla Via 1983, 1986; Gottstein Matočec and Kerovec 2002; Gottstein Matočec et al. 2006), benthic opportunistic omnivore decapod species (Gottstein Matočec et al. 2006), with quick response metabolic rhythm and osmoregulation (Dalla Via 1983, 1986).

Due to the *P. antennarius* habitat fragmentation and its high adaptability, the species seems to be useful for the study of shaping patterns concomitant to varying ecological conditions. The present study aims at elucidating potential intraspecific differences, sexual dimorphism and nuptial morphologic changes of north-western Greek populations of *P. antennarius*, applying morphometry and multivariate methods.

Material and methods

Study sites

Four ecologically important ecosystems of north-western Greece, one lentic and three lotic, were selected for the present morphological study. Three study sites were located near the estuaries of Louros, Thiamis and Acheron Rivers, and two study sites at littoral and pelagic zones of Lake Pamvotis. More specifically, the sampling was carried out at the following locations: (1) s1, Louros River, depth: 0.5 m (39°03′14″N, 20°46′26″E), (2) s2, Thiamis River, depth: 0.5 m (39°32′28″N, 20°09′76″E), (3) s3, Acheron River, depth: 0.5 m (39°13′96″N, 20°29′14″E), (4) s4, Pamvotis Lake, depth: 0.5 m (39°39′20″N, 20°52′14″E) and (5) s5, Pamvotis Lake, depth: 7 m (39°40′10″N, 20°53′20″E; Fig. 1). Louros River with 75 km total length has an altitude ranging from 0 to 1400 m above the sea level, and a mean flow of 23.8 m^3/s. The total river basin occupies an area of 780 km^2 and its mean depth is 2.5 m. The river has small reservoirs but is under strong anthropogenic stress, influenced by external and internal organic loads, and urban pollution (Dafis et al. 1997; Katsaounos et al. 2007). The characteristic vegetation of the river includes the reeds *Typha angustifolia*, *Phragmites australis* and submerged macrophytic species of the genera *Potamogeton* and *Myriophyllum.* Thiamis River, with 115 km total length, is one of the most important rivers of the country in terms of water quantity. The river has a mean flow of 57 m^3/s, a mean depth of 2.7 m and its total basin occupies an area of 1747 km^2 (Zalidis and Mantzavelas 1994). The river flow shows important fluctuations along its altitudinal profile (0–1300 m), because of the small waterfalls, gorges, reservoirs and intense anthropogenic stress (Zalidis and Mantzavelas 1994). *T. angustifolia*, *P. australis* and species of the genera *Potamogeton*, *Polygonum* and *Ranunculus* are among the characteristic riverine vegetation (Zalidis and Mantzavelas 1994). Acheron River has 50 km total length, situated southern with an altitudinal profile ranging from 0 to 1600 m. The river shows uninterrupted flow, lacking reservoirs constructions (Dafis et al. 1997). Its mean depth is about 2 m. *T. angustifolia* and *P. australis* have been recorded as characteristic aquatic macrophytic species. Lake Pamvotis is a shallow (mean depth of 4.5 m and maximum of 7.5 m) eutrophic lake, located 470 m above the sea level. The lake occupies an area of 22.8 km^2 and is influenced mostly by external and internal organic loads (Kagalou

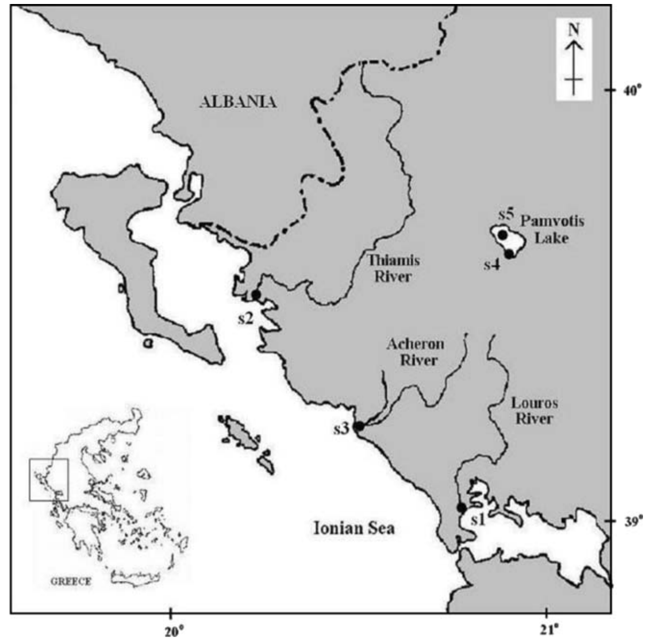

Fig. 1. Map indicating the study sites.

et al. 2003, 2007). The main lake water chemistry parameters were studied by Romero et al. (2002). It is a small lake with intense pollution from discharge of domestic sewages, sediment deposit, agricultural areas and biomanipulation processes, vulnerable to heavy-metal pollution (Kalfakakou and Kallistratos 1987; Papagiannis et al. 2004; Kagalou et al. 2006). The lake is characterised by dense reed beds of *T. angustifolia* and *P. australis*. Furthermore, floated vegetation of *Nymphoides peltata* and *Lemna minor*, and submerged macrophytes of *Myriophyllum spicatum*, *Polygonum amphibium*, *Ranunculus trichophyllus* and *Phalaris arundinacea* have been recorded (Stefanidis and Papastergiadou 2007; Kagalou et al. under publication).

Shrimp sampling – morphological assessment

Shrimp sampling took place near the aquatic submerged vegetation. The specimens were collected by means of a hand net and traps with a mesh size of 2 mm. The samples were collected during April 2004. The shrimps caught were preserved on site with 4% formalin solution. Sex identification was made through stereomicroscopic inspection of the first and second pairs of pleopods (Descouturelle and Frentz 1970; Descouturelle 1971). Eight morphometric measurements were made on each specimen (Fig. 2): total length (TL), carapace length (CL), carapace height (CH), rostral length (RL), second pleon segment height (SSH), sixth pleon segment length (SISL), telson length (TEL) and telson width (TEW). The body lengths were measured using digital calliper ($\pm$0.01 mm). Ovigerous females concerted as a discrete biological category from females, for the study of any nuptial differentiation. Furthermore, juveniles were excluded from the morphological assessment, so that the state of maturity or other factors could not influence the observed differences.

Statistics

A total of 638 individuals were measured during this study. Analysis of variance (ANOVA; Zar 1984) was firstly carried out in order to study the CL among the biological categories (males, females and ovigerous females). Secondly, all the measurement values were $\log_{10}$ transformed to meet the normality assumption. The allometric equation $Y = aX^b$ was used to remove the effect of CL (X) variation on characteristic length (Y), in each sample (Tzeng 2004). All characteristics were standardized according to: $Yi^* = Yi(X/Xi)^b$, where Yi* is the standardized measurement length of the *i*th specimen, Yi the measured length of the *i*th specimen, Xi the measured CL of the *i*th specimen, X the mean value of the CLs of the examined specimens and b the exponent of the allometric equation $Y = aX^b$. The exponent b was determined by applying non-linear regression on the equation $Y = aX^b$. After standardization of values, ANOVA was carried out in order to test the statistical significance of each measurement in relation to the site and biological category.

Multivariate analyses [principal component analysis (PCA) and discriminant function analysis (DFA)], were used to identify morphological differences among the biological categories and sampling sites, both of which are useful in analysing intraspecific variations (Thorpe 1980). PCA was performed to detect the morphometrical differences among the biological categories and samples and to determine the contribution of each

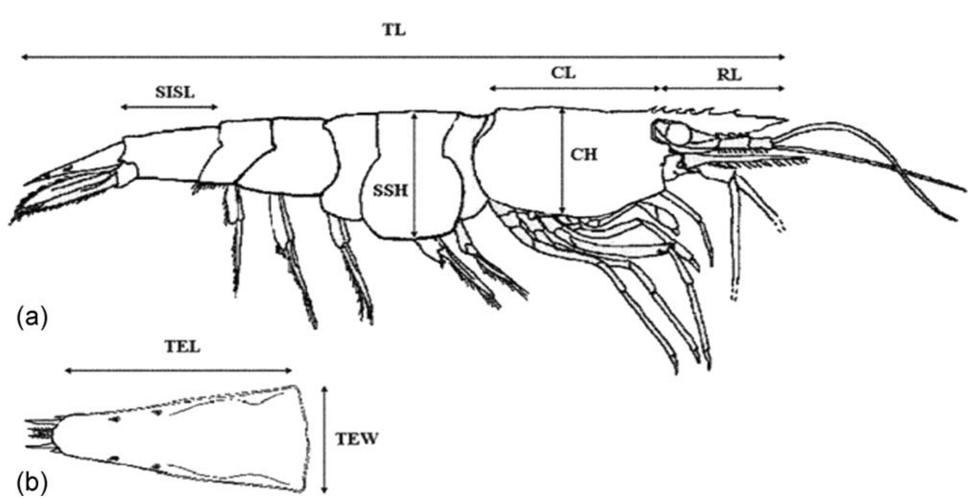

Fig. 2. Morphometric measurements taken on each individual of Palaemonetes antennarius: (a) lateral view of the specimen and (b) dorsal view of telson; TL, total length; CL, carapace length; CH, carapace height; RL, rostral length; SSH, second abdominal segment height; SISL, sixth abdominal segment length; TEL, telson length and TEW, telson width.

variable to the differentiation. DFA was used to obtain a function for discriminating and classification of the known groups. DFA was performed by using the stepwise method, in which each variable was included in the analysis until the discriminant power was not further improved. The variables with F-value > 1 were considered to contribute to the DFA (Lu and Bernatchez 1999; Saint-Laurent et al. 2003). Scatterplots of canonical scores in two-dimensional space were constructed for visual detection of groups. Differences among biological categories and samples were assessed with Wilk's λ and the associated F- and P-statistics. All statistical analyses were performed by the SPSS software (ver 15.0).

Results

The mean CLs were varied from 5.74 to 8.91 mm (Table 1). Statistically significant differences of the CL were found between sexes ($F = 137.1$; $P < 0.001$), sites ($F = 98.6$; $P < 0.001$) and their interaction ($F = 7.4$; $P < 0.001$). Ovigerous females from lotic habitats demonstrated larger CL (8.75 ± 0.55 mm) than females (7.15 ± 1.20 mm) and males (6.11 ± 0.91 mm). In the lentic littoral habitat, female specimens showed higher values for CL than male specimens while at the pelagic station the mean values of CL did not show any significant differences between the sexes ($F = 10.4$; $P < 0.001$). Moreover, males and females from Acheron River had the lowest values in CL, while the specimens from Lake Pamvotis had the highest (Table 1, Fig. 3).

After the standardization of measured variables, the two-way ANOVA showed that each measurement was statistically significant in reference to the sampling site ($F = 53.4$; $P < 0.001$), sex ($F = 79.5$; $P < 0.001$) and their interaction ($F = 6.4$; $P < 0.001$). More specifically, the relative TL demonstrated higher values in males than females. Only ovigerous females from the Acheron River demonstrated larger relative TL than males. Relative CH was found to have generally higher values in ovigerous females than males (Table 2). Relative RL showed the highest value in specimens from the Lake Pamvotis at the pelagic station and the lowest in the Acheron River. Relative SSH had the highest values for the ovigerous females in the Louros and Acheron Rivers, while relative SISL and TEL had the highest values for specimens in the Lake Pamvotis and lowest in the Thiamis River (Table 2).

PCA, after varimax rotation, extracted two principal component (PC) factors with eigenvalues > 1, explaining 61.77% of the variance. According to the factor loadings for each morphometric variable (Table 3), it can be assumed that PC I expressed characters mainly associated with appendages' growth (RL, sixth somite length, TEL and TEW) whereas PC II expressed variables exclusively associated with the body heights (carapace height and second somite height). The vector plot of the measured variables, for the two PCs and the PC profile plots are given in Fig. 4. PC I showed the same values for male and female specimens and

Table 1. Sampling site, sample size, means, standard deviation and ranges of carapace length (CL, mm) by sex

Sampling site	Sex	N	CL (mm)	
			Mean (SD)	Range (min−max)
Louros river (s1)	M	64	6.11 (0.91)	4.62–9.37
	F	36	7.15 (1.20)	4.70–9.01
	OF	28	8.75 (0.55)	7.85–10
Thiamis river (s2)	M	50	5.74 (0.52)	4.78–6.78
	F	51	6.81 (0.96)	4.88–8.92
	OF	29	7.50 (0.59)	6.32–8.60
Acheron river (s3)	M	50	6.11 (0.30)	5.48–6.85
	F	46	6.63 (0.95)	4.43–9.11
	OF	12	7.50 (0.59)	6.70–8.51
Lake Pamvotis (littoral) (s4)	M	75	6.34 (0.69)	5.10–8.67
	F	75	8.23 (0.92)	5.62–10.7
Lake Pamvotis (pelagic) (s5)	M	50	8.05 (0.68)	5.97–9.51
	F	73	8.91 (1.21)	6.86–11.79

M, males; F, females; OF, ovigerous females; N, number of individuals.

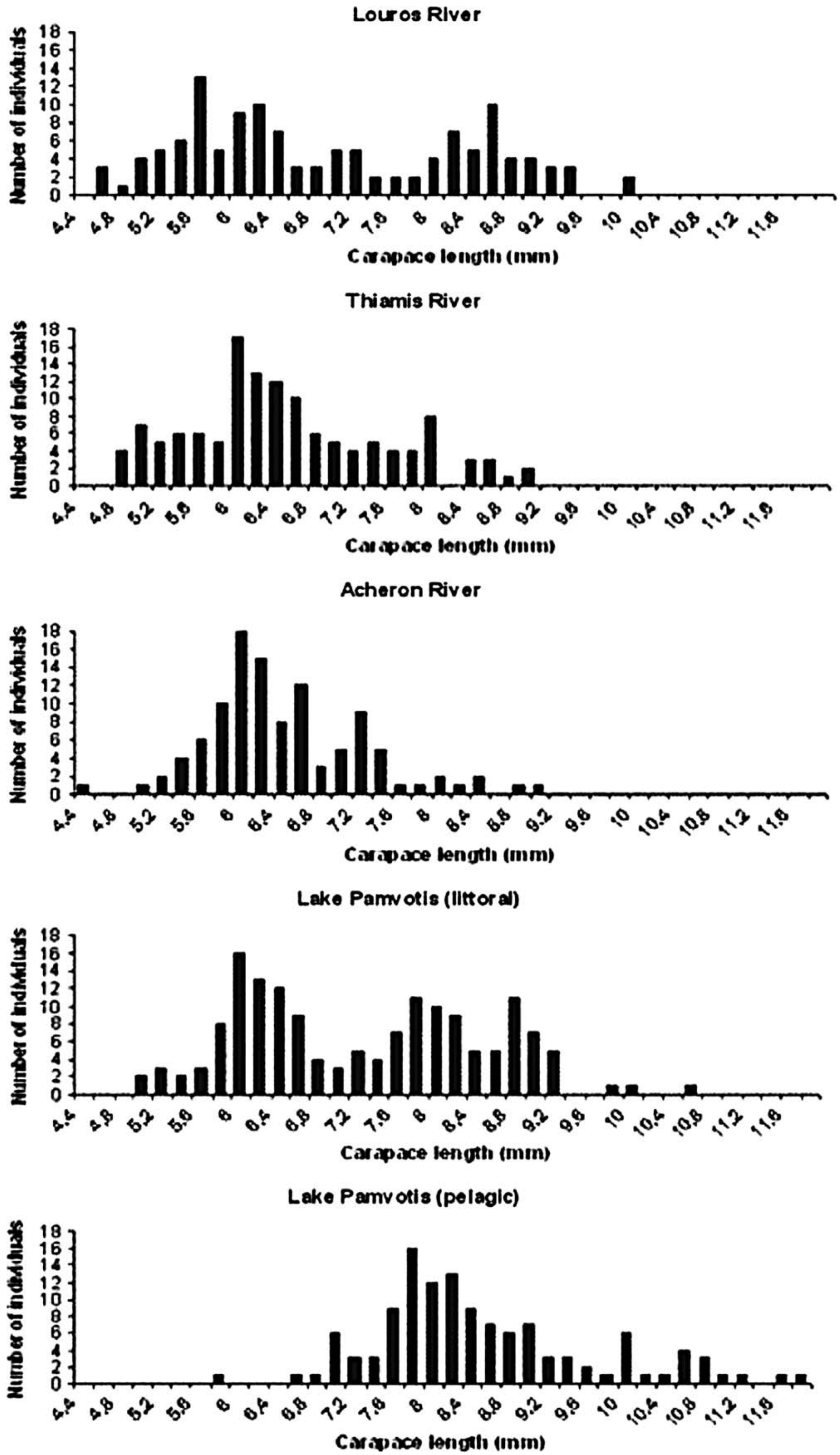

Fig. 3. Size frequency distribution of *Palaemonetes antennarius* specimens given by the study sites.

Table 2. Means and 95% coefficient interval (±) for the measured morphological features, after standardization, given by site and sex

Characters	Sex	Louros river		Thiamis river		Acheron river		Lake Pamvotis (l)		Lake Pamvotis (p)	
		Mean	95% CI (±)	Mean	95% CI (±)	Mean	95% CI (±)	Mean	95% CI (±)	Mean	95% CI (±)
TL	M	3.47	0.01	3.45	0.01	3.45	0.01	3.48	0.01	3.48	0.01
	F	3.42	0.01	3.40	0.01	3.45	0.01	3.42	0.01	3.42	0.01
	OF	3.39	0.01	3.40	0.01	3.47	0.02	–	–	–	–
CH	M	2.57	0.01	2.53	0.01	2.56	0.01	2.50	0.01	2.59	0.01
	F	2.59	0.01	2.59	0.01	2.61	0.01	2.56	0.01	2.59	0.01
	OF	2.65	0.01	2.61	0.01	2.67	0.02	–	–	–	–
RL	M	2.69	0.01	2.69	0.01	2.64	0.01	2.72	0.01	2.75	0.01
	F	2.68	0.01	2.66	0.01	2.66	0.01	2.72	0.01	2.74	0.01
	OF	2.69	0.01	2.69	0.01	2.70	0.02	–	–	–	–
SSH	M	2.58	0.01	2.55	0.01	2.54	0.01	2.53	0.01	2.60	0.01
	F	2.57	0.01	2.56	0.01	2.58	0.01	2.57	0.01	2.59	0.01
	OF	2.71	0.01	2.69	0.01	2.72	0.02	–	–	–	–
SISL	M	2.47	0.01	2.46	0.01	2.45	0.01	2.52	0.01	2.54	0.01
	F	2.46	0.01	2.44	0.01	2.46	0.01	2.50	0.01	2.53	0.01
	OF	2.51	0.01	2.48	0.01	2.49	0.02	–	–	–	–
TEL	M	2.56	0.01	2.53	0.01	2.52	0.01	2.59	0.01	2.61	0.01
	F	2.56	0.01	2.51	0.01	2.54	0.01	2.59	0.01	2.63	0.01
	OF	2.59	0.01	2.56	0.01	2.56	0.02	–	–	–	–
TEW	M	1.97	0.01	1.98	0.01	1.93	0.01	2.02	0.01	2.05	0.01
	F	2.01	0.02	1.99	0.01	1.95	0.01	2.04	0.01	2.06	0.01
	OF	1.99	0.02	2.02	0.02	2.01	0.03	–	–	–	–

M, males; F, females; OF, ovigerous females.

Table 3. Factor loadings of principal component analysis (PCA) for each morphometric variable on the two extracted PCA factors after varimax normalized rotation

Characters	PC I	PC II
Total length	0.209	−0.527
Carapace height	0.098	0.860
Rostral length	0.824	−0.052
Second somite height	0.286	0.810
Sixth somite length	0.812	−0.001
Telson length	0.842	0.031
Telson width	0.666	0.140

PC I, first principal component; PC II, second principal component.

slightly higher values for ovigerous females. PC II exhibited higher values in ovigerous females and lower in males. Among the study sites, PC I showed the highest value in the pelagic site of Lake Pamvotis (s5) and the lowest in the Acheron River (s3). PC II exhibited higher values in the specimens from the Louros River (s1) and lower values in the littoral station of Lake Pamvotis (s4).

The position of group centroids, after running the DFA is given in Table 4. Summary statistics demonstrated that for the male specimens, DFA I accounted for 69.9%, DFA II accounted for 23.6% while DFA III and IV accounted for 5.1% and 4.1%, respectively. Correspondingly, for the female specimens, DFA I counted for 84.1%, DFA II for 11.8%, DFA III only for 3.2% and DFA IV for 0.9% additionally. Finally, for the ovigerous females, DFA I and II accounted rather highly for 57.8% and 42.2%, respectively. The structure matrix for the measured variables (Table 5) revealed that some variables have strong correlation with DFA I and II. Specifically, for males, two variables (RL and SISL) were highly correlated with DFA I and two variables (CH, SSH) with DFA II. For female specimens, four variables (CH, RL, SISL and TEL) were correlated almost equally with DFA I and two variables (CH and TEL) were highly correlated with DFA II. Finally, for ovigerous females, the largest absolute

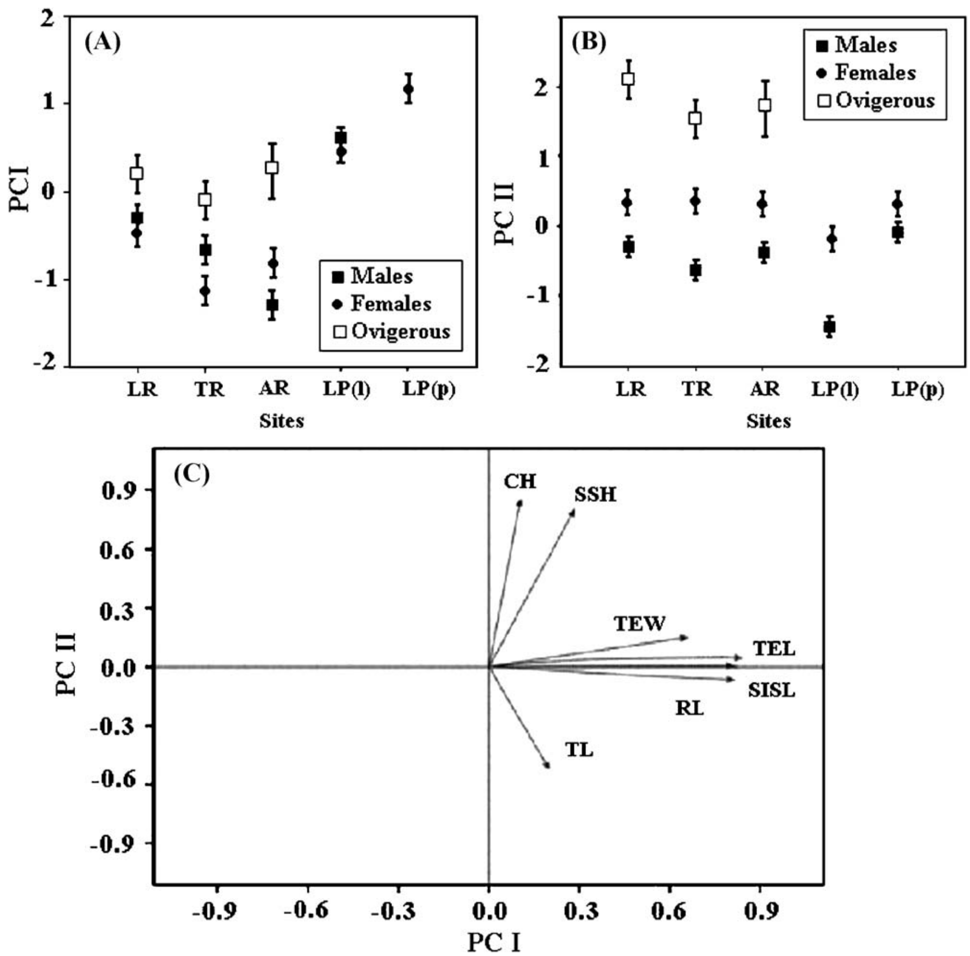

Fig. 4. (A, B) Profile plots of estimated marginal means of PC I and PC II, respectively, given by sampling site and biological category. The bars indicate 95% CI (±) of the means. (C) Vector plot of the measured variables, for PC I and PC II. LR, Louros River; TR, Thiamis River; AR, Acheron River; LP(l), Lake Pamvotis (littoral); LP(p), Lake Pamvotis (pelagic); M, males; F, females; O, ovigerous females; TL, total length; CL, carapace length; CH, carapace height; RL, rostral length; SSH, second abdominal segment height; SISL, sixth abdominal segment length; TEL, telson length and TEW, telson width.

correlation of the variable concerning body length was present in DFA I with higher loading. In Fig. 5, the scatter plots of DFA scores for the study sites are given by sex.

Discussion

The present study attempted to support the hypothesis that populations of *P. antennarius* living in different freshwater and estuarine habitats could exhibit morphological differentiation under the influence of different environments. Through minimisation of additional variances by means of size standardization and data transformation, the application of multivariate statistical analyses figured out the discrimination of the five populations of the natant decapod *P. antennarius*.

First of all, based on sexual dimorphism, females and ovigerous females were found to be larger than males in all studied populations (Table 1). Numerous publications suggest that size sexual dimorphism is very common for species from the Palaemonidae group (e.g. Rodriguez 1981; Bernard and Froneman 2005). More specifically, previous studies (Holthuis 1961; Cottiglia 1983) have shown that the larger female body size in *P. antennarius* specimens is characteristic of the species populations.

Among the study sites, male and female specimens of *P. antennarius* were found to be larger in Lake Pamvotis and smaller in Thiamis River (Table 1, Fig. 3). Lake Pamvotis is a small lake, which has been characterized as eutrophic to hypertrophic (Kagalou et al. 2003). According to Tzeng (2004), the allometric growth is affected by genetic and/or environmental factors. Thus, the observed differences could be attributed to the trophic state and the nutrient loadings of the studied ecosystems.

For the standardized variables, relative RL, SISL, TEL and TEW appear to be correlated to the study

Table 4. Position of group centroids in discriminant function analysis

Ecosystems	DFA I	DFA II	DFA III	DFA IV
Males				
Louros R.	0.775	0.639	0.042	0.384
Thiamis R.	1.117	0.648	0.835	0.092
Acheron R.	2.306	0.059	0.558	−0.241
L. Pamvotis (littoral)	1.774	1.098	0.224	0.036
L. Pamvotis (pelagic)	1.755	1.537	0.213	0.113
Females				
Louros R.	1.064	0.022	0.250	0.456
Thiamis R.	2.024	0.795	0.344	−0.182
Acheron R.	2.284	1.029	0.073	0.367
L. Pamvotis (littoral)	1.255	0.604	0.428	0.018
L. Pamvotis (pelagic)	2.088	0.539	0.308	0.070
Females ovigerous				
Louros R.	−0.935	1.115	−0.935	1.115
Thiamis R.	−0.261	−1.313	−0.261	−1.313
Acheron R.	2.812	0.571	2.812	0.571

DFA I–IV, first to fourth discriminant function scores.

Table 5. Discriminant function analysis on sexes separated

Characters	DFA I	DFA II	DFA III	DFA IV
Males				
TL	0.160	0.012	0.327	0.639
CH	0.160	0.752	0.277	0.336
RL	0.540	0.043	0.634	0.061
SSH	0.351	0.449	0.475	0.405
SISL	0.522	0.035	0.361	0.519
TEL	0.374	0.139	0.380	0.331
TEW	0.232	0.083	0.361	0.288
Females				
TL	0.168	0.368	0.758	0.162
CH	0.432	0.592	0.587	0.194
RL	0.420	0.268	0.002	0.256
SSH	0.255	0.151	0.003	0.176
SISL	0.586	0.103	0.870	0.222
TEL	0.449	0.565	0.198	0.482
TEW	0.343	0.460	0.160	0.041
Females ovigerous				
TL	1.012	0.001	–	–
CH	0.175	0.792	–	–
RL	0.042	−0.289	–	–
SSH	−0.227	0.246	–	–
SISL	−0.093	0.074	–	–
TEL	−0.451	0.655	–	–
TEW	0.224	−0.612	–	–

Structure matrix of discriminant loadings. DFA I–IV, first to fourth discriminant function scores; TL, total length; CL, carapace length; CH, carapace height; RL, rostral length; SSH, second abdominal segment height; SISL, sixth abdominal segment length; TEL, telson length and TEW, telson width.

area, while relative SSH and CH show correlation to the sex. Although Kapiris and Thessalou-Legaki (2001) found the rostrum variability to be correlated to sex, maturity and size, Burukovsky (1972) reported that several shrimp species show strong rostral variability regarding different types of habitats. On the other hand, morphometric characters, such as the height of the abdominal somites, have been related to sex, due to special formations of the caridean female pleon for reproductive purposes (Schram 1996; Mariappan and Balasundaram 2004).

PCA scores show that higher growth of appendages (PC I) is found in specimens from Lake Pamvotis (s4 and s5), and in ovigerous females from estuarine habitats (s1–s3). According to Schram (1996) this could be attributed to the fact that the appendage growth is usually related to the reophilic habitat profile and avoidance of predators. Lake Pamvotis has a high fluvial profile with a lot of reophilic species (Leonardos et al. 2008). On the other hand, estuarine environments are habitats with higher predation risk than enclosed lentic habitats (Wolff 1983). Regarding PC II scores among the studied ecosystems, only specimens from lentic littoral site demonstrated lower values. Regarding the studied morphometrical variables, specimens from the Acheron River showed low values for SISL, TEL and TEW, possible due to the restricted delta area. Specimens from estuarine sites showed high relative body heights (CH, SSH), a fact that could be attributed to high reproductive profile. Moreover, morphological variables related to the growth of appendages (RL, SISL and TEL) generally show higher values in ovigerous females with greater body mass. This could be attributed to the hypothesis that during reproductive period, ovigerous females migrate to the lower estuarine parts of the river and are generally vulnerable to predation (Agard 1999). This sex-related phenotypic plasticity is possibly shown at species which try to exceed the energetic cost of reproductive migration and predation risk, by forming a powerful caudal fan (TEL, TEW, sixth somite length).

In reference to DFA, males are discriminated better by DFA I, which is related to variables such as RL and sixth somite length. Female and ovigerous female specimens are discriminated by variables referring to body heights and telson growth. Among the study sites, the population from Louros River shows lower values for DFA I and II, due to the fact that specimens from the Louros River are generally smaller. DFA II, which is related to body heights and fecundity, shows higher values in female specimens from the Lake Pamvotis and the Acheron River. This could be explained because of the higher body growth of Lake Pamvotis specimens. Furthermore, high fecundity profile is demonstrated in the Acheron population due to restricted habitats

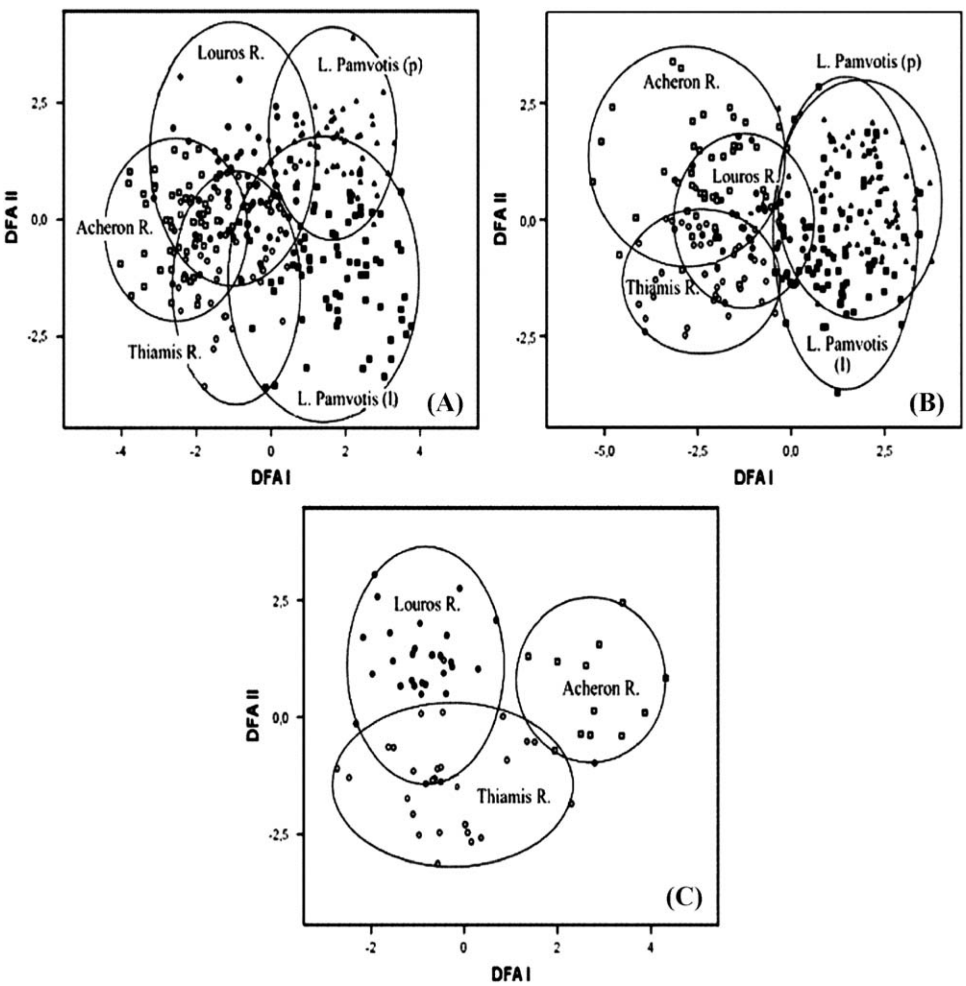

Fig. 5. Scatter plots of discriminant function analysis scores (DFA I and DFA II only) for the study sites are given by biological category: (A) males, (B) females) and (C) ovigerous females. DFA I and II: first and second functions of discriminant analysis; L, lake; R, river; p, pelagic; l, littoral.

and higher predation risk than in other estuarine environments.

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